



An early Miocene manatee from Colombia and the initial Sirenian invasion of freshwater ecosystems

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ABSTRACT

Potamosiren magdalenensis Reinhart, is an extinct species of manatee (Sirenia, Trichechidae, Trichechinae), which has only been recorded for the middle Miocene Honda Group, in the La Venta area (Huila Department, Colombia). A new specimen referable to *Potamosiren* cf. *P. magdalenensis* is reported herein, collected from the early Miocene Barzalosa Formation. This unit crops out in the Pubenza locality, at the Tocaima municipality of the Cundinamarca Department, Colombia. The material described here represents the first evidence of a mammal from the Barzalosa Formation, the earliest record of *Potamosiren* so far reported and one of the only two trichechid records for the early Miocene of South America. The new specimen adds to a small but growing record of extinct trichechids, increasing the fossil record of this group in South America and allowing us to further explore their evolutionary history. The early Miocene appearance of trichechines coincides geographically and temporally with the onset of the Pebas Mega-Wetland System, which likely provided favourable conditions for the invasion of freshwater ecosystems of this group of fully aquatic mammals. Finally, the depositional environments represented by the Barzalosa Fm and a review of the fossil record of trichechines further support the notion that manatees have had a close association with freshwater systems since early in their evolutionary history, and that reinvasion of marine ecosystems did not occur until much later.

1. Introduction

Sirenians are the only lineage of fully aquatic, herbivorous mammals. Evolving from terrestrial ancestors, sirenians have colonized both freshwater and shallow marine environments in tropical and subtropical waters (Domning, 2001a). This group is represented by the ‘sea cows’ in the extant families Dugongidae (dugongs) and Trichechidae (manatees), as well as by the Eocene Prorastomidae and Protosirenidae, which may be paraphyletic, and other stem taxa formerly placed in the Dugongidae (see Velez-Juarbe and Wood, 2019). In contrast to extant species, prorastomids, protosirenids and *Sobrarbesiren* were pig-sized, four-legged, amphibious herbivores (Domning, 2000, 2018; Díaz-Berenguer et al., 2020).

The oldest fossil records of sirenians are prorastomids from the middle Eocene of Jamaica (Savage et al., 1994; Domning, 2001a) and middle Eocene of Senegal (Hautier et al., 2012), and other sirenians of uncertain affinities from the early–middle Eocene of Tunisia (Benoit et al., 2013) and middle Eocene of Spain (Díaz-Berenguer et al., 2018). Prorastomidae are restricted to southeastern North America, Jamaica and western Africa, while the Protosirenidae were a widespread group during the Eocene, being found in India, Pakistan, and several localities in Europe, North America and Africa (e.g. Richard, 1946; Domning, 1982; Domning et al., 2017; Savage et al., 1994; Domning, 2001a, 2001b; Bajpai et al., 2009; Beatty and Geisler, 2010; Hautier et al., 2012; Zalmout and Gingerich, 2012; Velez-Juarbe, 2014). A doubtful record from the Eocene of southern South America, in Argentina, is based on

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the reinterpretation of *Florentinoameghinia mystica* Simpson (1932), as a sirenian (Serenio, 1982), but that has since been dismissed based on morphological grounds (Domning, 2001b; Velez-Juarbe et al., 2012b). Another doubtful sirenian record has been reported for the middle Miocene of Colombia, *Lophiodolodus chaparralensis* Stirton (1947). This taxon, described on the basis of an isolated worn m3, was initially considered as *Mammalia incertae sedis*, being compared with the pecaries and didolodonts (Stirton, 1947), later assigned to Didolodontidae (Romer, 1967) and finally, doubtfully to the Sirenia (McKenna, 1956; Domning, 1982, 2001b).

The fossil record of extant sirenian families in Central and South America is scarce compared to the rest of the world. Dugongids are known from the early Miocene Pirabas Formation of Brazil and the Culebra Formation of Panamá (De Toledo, 1989; De Toledo and Domning, 1991; Velez-Juarbe and Wood, 2019); the middle Miocene Montera Fm of Peru (De Muizon and Domning, 1985); as well as from the late Miocene Urumaco, Pisco, Bahía Inglesa and Paraná formations of Venezuela, Peru, Chile and Argentina, respectively (Bianucci et al., 2006; Domning and Aguilera, 2008; Koyabu and Sánchez, 2012; Velez-Juarbe et al., 2012b). The trichechid fossil record is even scarcer, including occurrences in the early Miocene portion of the Pebas Formation, in Peru (Antoine et al., 2016); the middle Miocene Honda Group of Colombia (Domning, 1997); late Miocene Ituzzaingo and Urumaco formations of Argentina and Venezuela, respectively (Ameghino, 1883; Linares, 2004); Pleistocene of North America (Domning, 2005; Bell et al., 2020); and the late Pleistocene of the Amazon River Basin, in Brazil (Perini et al., 2020 and literature therein). However, some of these, such as the records of *Potamosiren* sp. and *Ribodon* sp. from the Socorro and Urumaco formations, respectively (Linares, 2004), still need to be described in detail to confirm their identity.

This work describes a new specimen referable to *Potamosiren*, an extinct trichechid genus previously recorded from the middle Miocene of Colombia (La Venta area, Huila Department). This new material, collected from the Barzalosa Formation (early Miocene, Colombia) by the Colombian Geological Service (former INGEOMINAS) during 2003–2005 field campaigns, represents the earliest record of the genus

and one of the earliest records for the family in South America. Thus, assuming a freshwater origin for sirenians (Benoit et al., 2013), this information allows for a more thorough discussion on the timing of reinvasion of sirenians to freshwater habitats and subsequent return to the oceans.

2. Geological setting

The early Miocene Barzalosa Formation crops out at the Pubenza locality (4°24'21"N, 74°42'12"E), in the municipality of Tocaima, Cundinamarca Department, Colombia (Fig. 1). In this locality, the Barzalosa Formation crops out as a mudstone sequence (Castillo Velasquez, 2003; Paramo, 2005).

The Barzalosa Formation is composed mainly of multicoloured mudstones, conglomerates and sandstones (De Porta, 1966). Conglomerates with clasts from underlying Cretaceous units and sandy matrix predominate in the lower portion of the unit. Overlying this section, there is a thick sequence dominated by multicoloured mudstones, with intercalations of sandstone and conglomerate. The upper portion of the unit is composed mainly of sandstones and conglomerates (Acosta et al., 2002; Castillo Velasquez, 2003).

The Barzalosa Formation has been considered Eocene to Miocene in age (De Porta, 1966). However, based on palynological data, Cadena et al. (2006) placed this unit within zone 34 of Jaramillo and Rueda (2004) and Jaramillo et al. (2006). This zone is equivalent to zone T13 of Jaramillo et al. (2011), indicating a late early Miocene age (Burdigalian: 16.5–17.7 Ma) for the Barzalosa Formation (De La Parra et al., 2019). Together with the Mugrosa and Santa Teresa formations, the Barzalosa Formation represents a large freshwater lacustrine system that occupied the Magdalena River Basin during the early Miocene (Ochoa et al., 2012; De La Parra et al., 2019).

Fossil vertebrates previously reported for this locality were collected by field crews from the Colombian Geological Survey (formerly INGEOMINAS) and were found in the middle mudstone sequence (Castillo Velasquez, 2003; Paramo, 2005). This fossil association is mainly represented by pleurodire turtles and crocodilians (Cadena et al.,

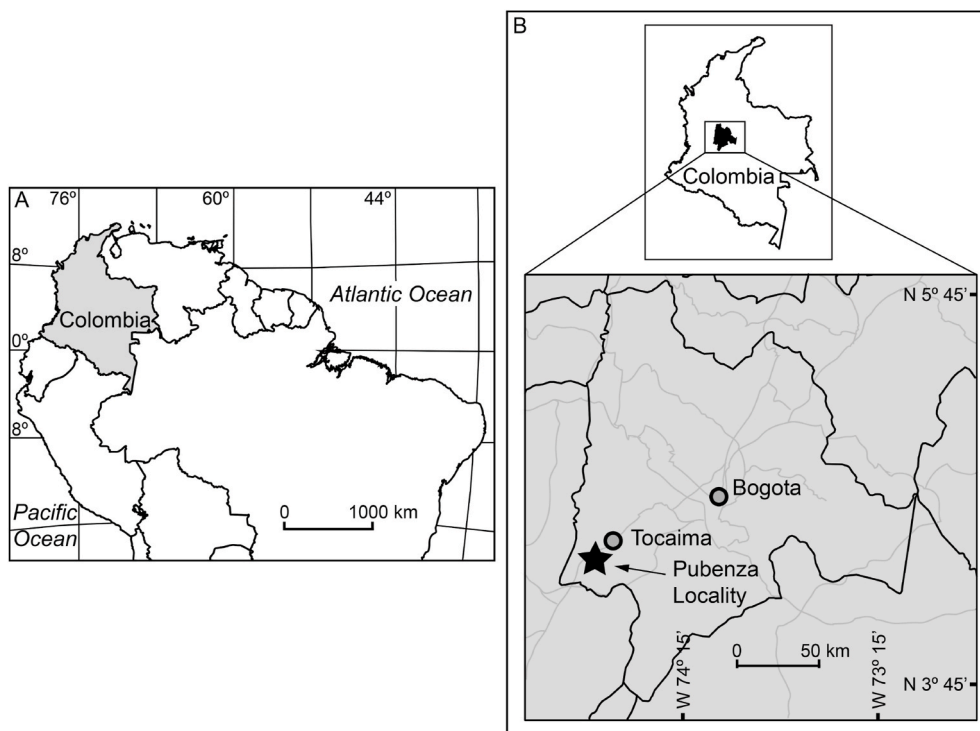


Fig. 1. Map of equatorial South America, showing: A, the geographical position of Colombia; B, the Pubenza locality in the Cundinamarca Department of Colombia.

2006, 2008; Moreno-Bernal, 2006), including podocnemidids, and the oldest record of the chelid *Chelus* (*C. colombiana*), as well as gavialoid and alligatorid crocodilians. The specimen described in this work, referable to *Potamosiren* cf. *P. magdalenensis* (Sirenia, Trichechidae), represents the first mammal fossil known from the Barzalosa Formation (see Discussion).

3. Material and methods

The dental nomenclature in this description follows Smith and Dodson (2003). Morphological data for comparisons were taken from direct observations on original specimens and published literature (e.g. Reinhart, 1951; Domning, 1997). Measurements were taken with digital calipers to the nearest 0.01 mm and are reported in millimeters. Additional measurements, for USNM 10870 and IGM 250927, were taken from previous works (Kellogg, 1966; Domning, 1997).

For the phylogenetic analysis we used a modified version of the character state matrix of Velez-Juarbe and Wood (2019). Because our focus is to show relationships amongst manatees and ecological habitat preference across Sirenia, we removed a number of mainly stem taxa (Pan-Sirenia sensu Velez-Juarbe and Wood, 2019), but added the recently described *Trichechus hesperamazonicus* Perini et al. (2020). This resulted in two outgroup taxa, namely Proboscidea, represented by *Phosphatherium escuilliei* Gheerbrant et al. (1996) (see also Gheerbrant et al., 1998, 2005), and Desmostylia Reinhart, 1953, represented by *Cornwallius sookensis* Cornwall (1922) (see also Beatty, 2009), and a total of 44 ingroup taxa (Supplementary material S1). We also updated character six, based on Domning and Beatty (2019), and added character 156 from Domning (1994). The analysis was performed in PAUP* (v. 4.0a; Swofford, 2020); all characters were treated as unordered and of equal weight. A heuristic search of 1000 replicates was performed using the tree bisection-reconnection (TBR) algorithm and using a backbone constraint tree based on the molecular phylogeny from Springer et al. (2015). Bootstrap values were obtained by performing 1000 replicates (Supplementary material S2).

3.1. Institutional abbreviations

IGMp, Colombian Geological Survey (formerly INGEOMINAS), Bogotá, Colombia, paleontology collection; LACM, Mammalogy Collection, Natural History Museum of Los Angeles County, Los Angeles, CA, USA; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington D. C., USA.

3.2. Other abbreviations

M/m, molar (capital and lower case letters refer to upper and lower teeth, respectively); dP, deciduous upper premolar; SALMA, South American Land Mammal Age.

4. Systematic paleontology

MAMMALIA Linnaeus (1758)

SIRENIA Illiger (1811) sensu Velez-Juarbe and Wood (2019)

TRICHECHIDAE Gill (1872) (Gray, 1821)

TRICHECHINAE Gill (1872) (Gray, 1821)

Potamosiren Reinhart (1951)

Potamosiren cf. *P. magdalenensis* Reinhart (1951)

(Fig. 2, Table 1)

Synonym: *Metaxytherium ortegense* Kellogg (1966), p. 93

4.1. Material

IGMp 450086, left maxilla fragment with the alveolus for the lingual root of the dP5, the three alveoli of the M1 (for one lingual and two labial roots) and nearly complete M2–3 (Fig. 2).

4.2. Stratigraphic and geographic range

Pubenza locality, municipality of Tocaima, Cundinamarca Department, Colombia (Fig. 1); Barzalosa Formation, early Miocene (Burdigalian: 16.5–17.7 Ma).

Table 1

Measurements of the new specimen described and materials mentioned for comparisons. All measurements in millimeters. Abbreviations: L (md), mesio-distal length; M1, first upper molar; M2, second upper molar; M3, third upper molar; W (m), mesial width; W (d), distal width.

Specimen	Locus	W (m)	W (d)	L (md)
IGMp 450086	M1	–	–	–
	M2	–	19.06	20.40
	M3	–	21.41	21.52
IGM 250927	M1	–	–	–
	M2	–	19.40	–
	M3	21.40	17.60	–
USNM 10870	M1	19.50	17.50	22.00
	M2	23.00	21.20	26.00
	M3	25.00	21.00	29.50

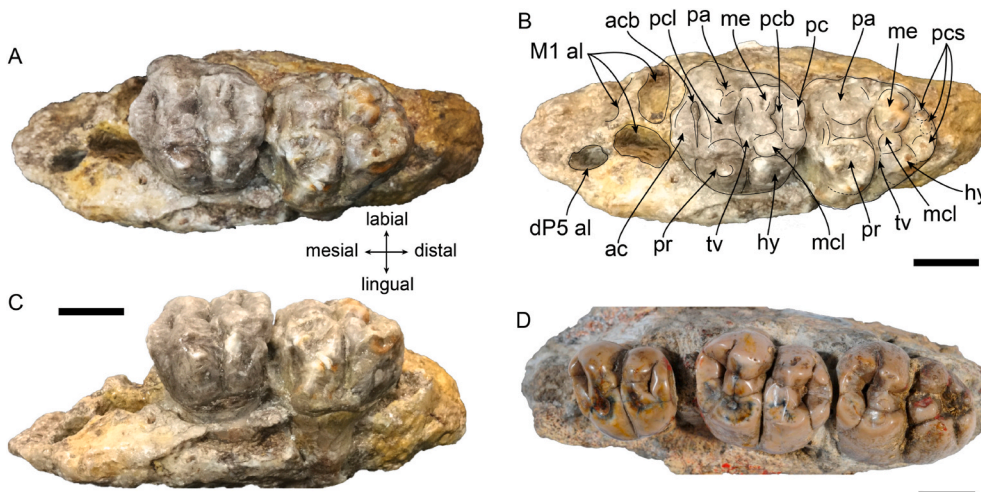


Fig. 2. Comparison between IGMp 450086 (*P. cf. P. magdalenensis*) and USNM 10870 (holotype of *Metaxytherium ortegense* –synonym of *P. magdalenensis*). IGMp 450086, left maxillary fragment with the alveolus of the lingual root of the dP5, the three alveoli of the M1 and nearly complete M2–3: A, occlusal view; B, scheme showing the main structures in occlusal view; C, lingual view. USNM 10870, left maxilla with M1–3: D, occlusal view. Abbreviations: ac, anterior cingulum; acb, anterior cingular basin; dP5 al, dP5 alveoli; hy, hypocone; M1 al, M1 alveoli; me, metacone; mcl, metaconule; pa, paracone; pcb, posterior cingular basin; pc, posterior cingulum; pcl, paraconule; pcs, posterior cusps forming the posterior cingulum; pr, protocone; tv, transverse valley. Scale: 10 mm.

4.3. Description

Four alveoli are present mesial to the preserved teeth. The lingual (and only preserved) alveolus of the dp5 is mesiodistally elongated, being ellipsoidal in section. Distal to this one, one of the alveoli of the M1 is present. It is roughly ellipsoidal, with the lingual margin concave and the labial margin convex, and larger than the alveolus of the dp5. These two alveoli of adjacent teeth are not aligned but set obliquely from each other. The two labial alveoli of the M1 are not completely preserved. However, the preserved portions indicate that they were more circular in outline and smaller than the lingual alveolus. They are similar in size to each other (~ 6 mm) and separated by a thick bony bridge. The mesiolabial alveolus is placed at the level of the embrasure between the lingual alveoli for the dp5 and the M1. The distolabial alveolus is distally aligned with the lingual one, extending mesially until around two thirds of its length.

The M2 is longer than wide (Table 1). The fractures of the maxilla expose the roots of the M2, allowing confirmation of the presence of two labial roots and one lingual as is usual in most sirenians. The anterior cingulum, located at the mesiolabial margin of the tooth, is incomplete, lacking a labial fragment of less than one-third of its total extension. It is well developed, being thick and extending from the mesiolingual face of the parastyle (this portion is absent) to the mesial face of the protocone. The anterior cingular basin is straight, deep and labiolingually elongated. The paracone is incomplete, lacking a labial portion. It is blunt, large and mesiolabially expanded. The parastyle is not distinguishable: the wear degree is high but there is not any signal of division between the paracone and a parastyle, maybe due to preservation conditions. However, the mesiolabial projection of the paracone is probably indicating its presence. The apex of the paracone is not clearly differentiable. However, there is an irregular cusp-like structure, worn and poorly preserved, placed between the protocone and the base of the paracone, which probably corresponds to the paraconule. The protocone is almost complete, with a fracture on the distolabial face. It is apparently larger than the paracone, though the difference in size is not clear because of the difficulty of identifying the boundaries between the paracone and parastyle.

The transverse valley divides the crown, in occlusal view, into a mesial and a distal portion. It is almost straight and runs labiolingually, extending lingually until the base of the crown, clearly separating the protocone from the hypocone. The distal portion of the crown is set at a higher level with respect to the mesial portion. This feature is better observed in lingual and labial view. The metacone is incomplete, lacking portions of the labial and occlusal surfaces. It is apparently smaller than the paracone, but the difference in size is not clear because of the lack of evidence of the limit between the paracone and parastyle. The metacone and metaconule are located in a position more lingual than the paracone and paraconule respectively. The metacone and hypocone are labiolingually aligned, while the metaconule slightly interrupts the transverse valley. The hypocone is incomplete, with a fracture on its mesial and labial faces. The preserved portions indicate that the hypocone was smaller than the protocone. The postcingulum is almost completely preserved, lacking only a small fragment at its labial end and another at the lingual one. It is clearly well developed but no accessory cusps are clearly identifiable. However, its labial and lingual ends are thicker than its medial portion, so it could be the case that two cuspules were present at these points. The distal cingular basin is similar to the mesial one in width and depth, though the latter looks mesiodistally broader due to its heavier wear.

The M3 is larger than the M2 (Table 1). Only the single lingual root is exposed through the bone. The mesial-most portion of the tooth is broken, so the structures located mesial to and at the level of the mesial cingular basin are poorly preserved. The paracone preserves only a small lingual portion and the base. There is not preserved evidence of a parastyle. The paraconule is almost complete (slightly eroded) on its occlusal and distal surfaces. However, its limits are more visible than in

the M2, showing a mesiodistally elongated (labiolingually compressed) shape and a clear contact with the paracone and protocone. The protocone is incomplete, preserving only part of the distal and distolingual faces, and a great part of the base (except a small mesiolingual portion).

The transverse valley has the same configuration as in the M2 but, as the metaconule is larger, its disruption of this valley is more evident. The difference in height between the mesial and labial halves of the crown is absent in the M3. As in the M2, the metacone and metaconule are located at a more lingual level than the paracone and paraconule respectively. The metacone is almost complete, lacking only a thin enamel layer from the labial face. It is apparently slightly smaller than the paracone. A short and deep vertical groove is present on the distal face of the metacone, ending at the distal cingular basin. A small structure is present near the metacone, in a mesiolabial position, but it is not clear if it is separated enough to be considered an independent structure, or if it is just a mesiolabial expansion of the metacone. The metacone is well differentiated from the metaconule, being separated by a wide deep groove, which distally ends in the distal cingular basin. The metaconule is closer to the hypocone than to the metacone, being separated only by a weak furrow. The hypocone is broken, lacking part of the lingual portion. It is smaller than in the M2, being smaller than the protocone and just slightly larger than the metaconule. The postcingulum is almost complete, except for a small fragment lacking at its labial end. It is well developed and thick, showing three cuspules: a large lingual cuspule, adjoined to the hypocone and apparently larger than it; a small cuspule (broken) in a medial position; and a much smaller labial cuspule, almost vestigial. It is lingually separated from the hypocone only by a weak furrow, similar to that which separates this last cusp from the metaconule. Labially, the postcingulum is interrupted before contacting the metacone because the distal cingular basin is labially open.

4.4. Wear facets

There are two confluent wear facets on the transverse valley of the M2: the mesial facet is placed on the distal faces of the paracone, paraconule and protocone; the distal facet comprises the mesial margin of the metacone, metaconule and probably the hypocone (the mesial face of the hypocone is broken). The distal cingular basin is similar to the mesial one in width and depth, though the latter looks mesiodistally broader due to the higher wear. There are no wear facets on the M3, indicating a later eruption.

5. Discussion

Fossil remains referable to *Potamosiren* have been previously reported only for the Honda Group (middle Miocene), in the La Venta locality (Huila Department, Colombia; Reinhart, 1951; Kellogg, 1966; Domning, 1997). Additional, undescribed sirenian remains have been reported from the Castilletes Formation in the Guajira Peninsula of Colombia (Moreno et al., 2015). The late early to early middle Miocene (c. 17.3–14.5 Ma) age of this unit (Hendy et al., 2015) is roughly coeval to that of the Barzalosa Formation. Another undescribed record from the early Miocene of South America is a trichechine molar from the lower Pebas Formation in Peru (Antoine et al., 2016). Therefore, the specimen herein described represents the earliest record of *Potamosiren* known to date as well as one of the earliest occurrences of trichechines.

Furthermore, this material also represents the first confirmed record of fossil mammals from the Barzalosa Formation. Previous reports from the Chaparral area (Tolima department, Colombia), including *Lophiodolodus chapparralensis* (Sirenia?; initially classified as a sloth), *Protheosodon* sp. (Litopterna), *Proadinothereum* sp. (Notoungulata) and an astrapotheriid, supposedly came from this unit (Stirton, 1947). However, Stirton (1953) suggested the unit cropping out in that area would correspond to the Oligocene 'Tuné' Formation. According to the Texas Petroleum Company, this unit was included within the Gualanday Group, but Stirton (1953, p. 609) indicated that it would correspond to

the base of the Honda Group. The most current geological interpretation considers that the Tuné Formation (late Oligocene to early Miocene) conformably overlies the upper-most conglomerate of the Gualanday Group and is unconformably overlaid by the La Victoria Formation, which is considered the base of the Honda Group (Guerrero, 1997). In contrast to the well-known fossil mammal association from the Honda Group (middle Miocene, Laventan South American Land Mammal Age; Kay et al., 1997), mammals from the ‘Tuné’ and Barzalosa formations are scarcely known and only represented by the taxa described by Stirton (1953) and the *Potamosiren* specimen here reported, respectively.

Regarding the morphology of the material described here, both M2 and M3 are nearly completely preserved and they display a cusp pattern that is in general similar to dugongids and trichechids. However, the teeth of IGMp 450086 have very thick enamel, which is consistent with the morphology of specimens referred to the early trichechid *Potamosiren magdalenensis* (e.g. USNM 10870, holotype of the synonym *Metaxytherium ortegense*; Kellogg, 1966; Domning, 1997; Fig. 2). The molars of IGMp 450086 are smaller than those of USNM 10870 (Kellogg, 1966; Fig. 3), but the overall cusp pattern is similar, with a more prominent and thick anterior cingulum, and relatively open transverse valley, having a more attenuated constriction by the metaconule than is observed in most dugongids (Domning, 1988; Velez-Juarbe et al., 2012b). There are some characters which are difficult to interpret in IGMp 450086, since they were obscured by wear or state of preservation. Among them, the evident labial furrow between the parastyle and the paracone in the M2, or the morphology of the paraconule, which are distinctive of *P. magdalenensis*.

As explained above, despite the difference in size, the overall morphology of IGMp 450086 closely resembles that of *Potamosiren*. Since the bunodont and brachydont teeth stop their growth once they erupt, the difference in size with the larger referred specimen of *P. magdalenensis*, USNM 10870, is not attributable to distinct ontogenetic stage. Additionally, in contrast to other Trichechinae, such as the late Miocene *Ribodon limbatus* Ameghino (1883), or *Trichechus* spp., *Potamosiren* lacks the continual dental replacement (Gomes Rodrigues et al., 2011; Beatty et al., 2012) that would otherwise hinder the identification of ontogenetic differences. However, due to the lack of more specimens or stronger qualitative characters that could support IGMp

450086 as a new species of *Potamosiren*, the most parsimonious option is to consider this size difference as intraspecific variation. Some differences in size are also seen in the M3 of the specimen IGM 250927 where, according to measurements published by Domning (1997), is smaller than what is observed in USNM 10870 (see Table 1).

5.1. Sirenian invasion of freshwater ecosystems

The geochronologically oldest stem sirenian (pansirenian) consists of a petrosal found in early to middle Eocene (late Ypresian–early Lutetian) freshwater deposits at Djebel Chambi, Tunisia (Benoit et al., 2013). However, the group quickly adapted to marine environments and were capable of long-distance dispersal, as evidenced by the presence of *Prorastomus sirenoides* Owen (1855) and the quadrupedal *Pezosiren portelli* Domning (2001a) in middle Eocene (Lutetian) marine deposits in Jamaica. Since then, and with few exceptions (see below), stem and crown sirenians have been inhabitants of marine ecosystems in tropical and subtropical regions, including the presence of multispecies communities with no extant analogues (Domning, 2001b; Velez-Juarbe et al., 2012a).

Trichechids first appear in the fossil record during the late Oligocene where they are known from marine deposits in Germany, with later records from the early Miocene of Belgium and middle Miocene of France (Domning, 1996; Sorbi, 2008). Meanwhile, the earliest evidence of trichechids in the western hemisphere consists of a putative trichechine tooth recovered from the base of the Pebas Formation in Peru (Antoine et al., 2016). At this locality, the Pebas Fm. is interpreted as representing lacustrine environments with marine influence that were deposited during the early Miocene (Colhuehuapian SALMA; Antoine et al., 2016). Together with the Pubenza *Potamosiren*, they represent the earliest records of trichechines and the initial stages of a clade of crown sirenians invading freshwater ecosystems (Fig. 4). In stark contrast, crown odontocetes have entered freshwater ecosystems multiple times and in multiple lineages across their similarly long evolutionary history (Fordyce, 1983; Cassens et al., 2000; Hulbert and Whitmore, 2006; Geisler et al., 2011; Boessenecker and Poust, 2015; Bianucci et al., 2013; Pyenson et al., 2015; Boersma and Pyenson, 2016; Benites-Palomino et al., 2020). The answer to this discrepancy may lie in the more restricted dietary preferences of sirenians.

Sirenians have been primarily consumers of seagrasses throughout most of their evolutionary history (Clementz et al., 2003; MacFadden et al., 2004; Clementz and Sewall, 2011). As a result, their distribution is largely limited by the availability of this resource in shallow marine habitats around the world (Velez-Juarbe, 2014). The few notable exceptions are found within crown Sirenia, namely in hydrodamalines and trichechines. Hydrodamalines were restricted to the North Pacific basin where they thrived from the early Miocene until the extinction of Steller’s seacow (*Hydrodamalis gigas* Zimmermann, 1780) during the second half of the 18th century (Domning, 1978; Mclean et al., 1987; Domning and Furusawa, 1994; Carreño and Smith, 2007). Changes in ocean dynamics during the mid-late Miocene seems to have been responsible for a regional shift in the dominant marine flora of the North Pacific, from seagrasses to the cold-adapted kelps that are still ubiquitous in coastal environments in this region (Domning, 1978; Vermeij, 2018). This shift presumably had a role in the extinction of other marine mammal herbivores, specifically, dugongines and desmostylians by the late Miocene, while hydrodamalines seem to have made a clade-wide shift from seagrass to kelp consumers (Domning, 1978; Domning and Furusawa, 1994; Velez-Juarbe, 2014; Vermeij, 2018). This dietary shift in hydrodamalines, from the more fibrous seagrasses to the softer kelps higher up in the water column is reflected in the reduction of rostral deflection and complete loss of adult dentition in *Hydrodamalis* spp. (Domning, 1978; Domning and Furusawa, 1994; Springer et al., 2015).

The appearance of trichechines in South America coincides temporally and geographically with the early stages of the Pebas megawetland system; the unique palaeoenvironmental conditions of this

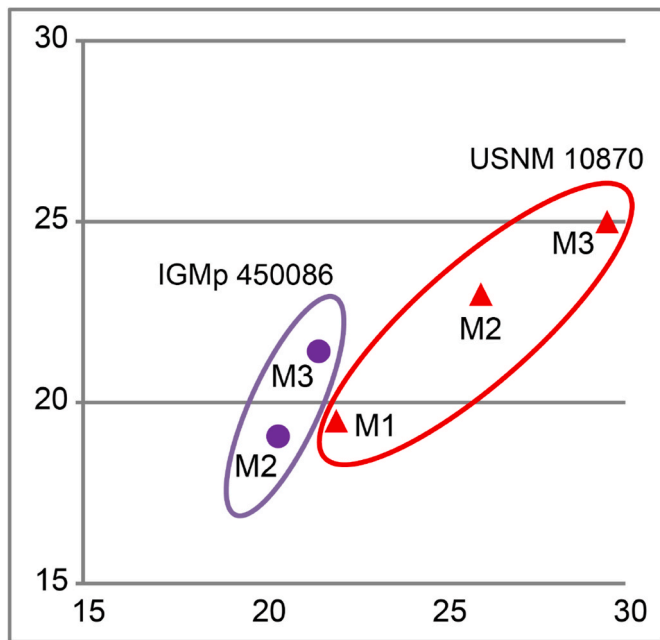


Fig. 3. Maximum labio-lingual and mesiodistal length (horizontal and vertical axes, respectively) of the upper molars of *Potamosiren*. Measurements of USNM 10870 taken from Kellogg (1966). Both axes in millimeters.

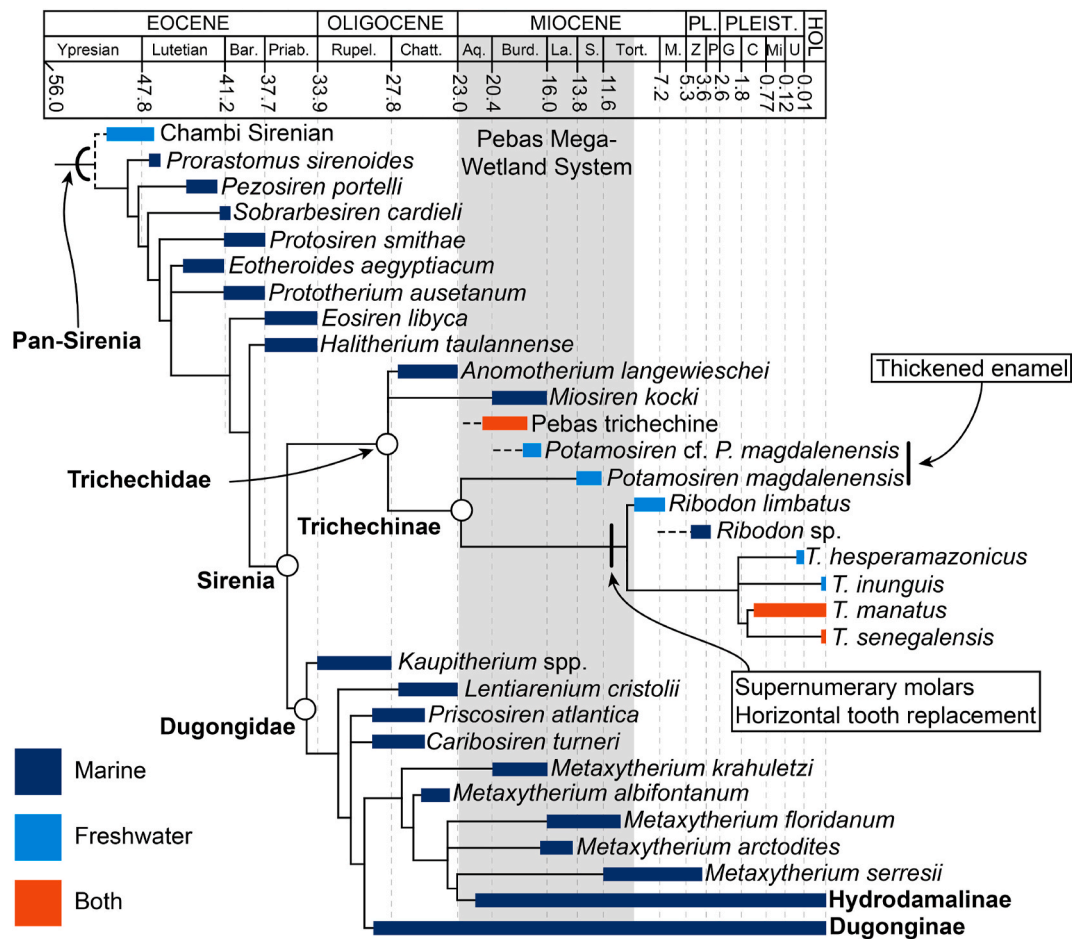


Fig. 4. Time-calibrated strict consensus tree of Sirenia (length = 261 steps; consistency index = 0.521; retention index = 0.768). Hydrodamalinae and Dugonginae are collapsed for ease of comparison; full tree available as [Supplementary file \(S2\)](#). Ages based on International Chronostratigraphic Chart, v 2020/03 (Cohen et al., 2013). Abbreviations: Aq., Aquitanian; Bar., Bartonian; Burd., Burdigalian; C., Calabrian; Chatt., Chattian; G., Gelasian; La., Langhian; M., Messinian; Mi, Middle Pleistocene; P., Piacenzian; Priab., Priabonian; Rupel., Rupelian; S., Serravallian; Tort., Tortonian; U., Upper Pleistocene; Z., Zanclean.

system likely offered the chance for sirenians as well as odontocetes to invade freshwater ecosystems (Fig. 4; Hoorn et al., 2010; Antoine et al., 2013, 2016; Boonstra et al., 2015; Benites-Palomino et al., 2020; Silva de Souza et al., 2021). Re-adaptation of sirenians to life in freshwater environments marked a shift in dietary preferences from seagrasses to other groups of aquatic-adapted macrophytes, including true grasses (Domning, 1982). In particular, an intensification of consumption of true grasses, which contain phytoliths, could accelerate tooth wear (Domning, 1982), as would an increase in sediment interaction while foraging for aquatic plants low in the water column (Beatty et al., 2012). Although *Potamosiren* retains the usual number of molars (M/m 1–3; Figs. 2 and 5A–B), the thickened enamel could be interpreted as an adaptation to counter this new, more abrasive diet. This would be akin to the thickened enamel seen *Desmostylus*, which, based on isotopic evidence, are interpreted as being consumers of seagrasses as well as freshwater and estuarine vegetation, more closely resembling the diet of extant Florida manatees (*Trichechus manatus latirostris* Harlan, 1824) than that of fully marine sirenians (Clementz et al., 2003). An alternative hypothesis offered by Domning (1997) is that the thickened enamel of *Potamosiren* served as an adaptation for crushing softer aquatic vegetation. Under this scenario, the shift to a more abrasive diet occurs later, leading to the evolution of supernumerary molars and horizontal tooth replacement that characterize the late Miocene *Ribodon limbatus* and *Trichechus* spp. (Figs. 4 and 5C–F; Domning, 1997).

During the early Oligocene through the early Pliocene dugongids proliferated in the west Atlantic and Caribbean region, including the

presence of multispecies communities (Domning, 2001b; Velez-Juarbe et al., 2012a, 2012b). The absence of marine trichechids along the western Atlantic and Caribbean regions may have been a result of these prolific dugongid multispecies communities which were already established by the early Oligocene. Meanwhile, trichechines seem to have been confined to freshwater ecosystems in South America, with their earliest occurrence in marine environments outside of the continent being represented by a partial maxilla referred to *Ribodon* sp. from North Carolina, presumably from Pliocene deposits (Figs. 4 and 5C; Domning, 1982, 1997, 2001b). Manatees continued to thrive in freshwater ecosystems in South America even after the disappearance of the Pebas mega-wetland system by the late Miocene, which seems to have led to the decline and even extinction of other aquatic tetrapods (Hoorn et al., 2010; Salas-Gismondi et al., 2015; Benites-Palomino et al., 2020; Silva de Souza et al., 2021). However, it seems that it was only near, or soon after, the extinction of dugongines from the western Atlantic and Caribbean region by the end of the Pliocene, that trichechines successfully returned to marine ecosystems, with the earliest record of *Trichechus* at about 1.3 Ma (Domning, 2005). The retention of the ecological and dietary flexibility that allowed trichechines to thrive in freshwater ecosystems in South America, and which sets them apart from all other known sirenians, living and extinct, facilitated their expansion across the Atlantic and Caribbean region (Domning, 2001b; Velez-Juarbe, 2014).



Fig. 5. Occlusal views of upper and lower dentition/toothrows of fossil and extant trichechines. A, left maxilla (USNM 10870) of *Potamosiren magdalenensis*; B, left mandible (UCMP 39471) of *P. magdalenensis*; C, right maxilla (USNM 167655) of *Ribodon* sp.; D, left mandible (MLP 41-XII-13-1721) of *Ribodon limbatus*; E, skull (LACM 72252) of *Trichechus manatus latirostris*; F, mandible (USNM 391907) of *Trichechus manatus bakerorum* Domning, 2005. Scale bars: 40 mm.

6. Conclusions

The material described is clearly identified as a trichechid (Mammalia, Sirenia), referable to *Potamosiren* cf. *P. magdalenensis*, being the earliest record of this genus, previously reported from the middle Miocene rocks of the La Victoria Formation, Honda Group (La Venta, Colombia). In addition, the specimen represents the first mammalian record for the Barzalosa Formation and also the earliest trichechid so far described for Colombia and one of the earliest sirenians described for South America.

The freshwater setting of the Barzalosa Formation supports the notion that the evolutionary history of trichechines is intimately tied to freshwater systems in South America. In particular, the onset of the Pebas mega-wetland system and the resulting palaeoenvironmental conditions may have provided the ideal settings for the invasion of freshwater ecosystems by this particular group of fully aquatic mammals. The shift from marine to freshwater environments seems to have led to significant changes in feeding preferences, resulting in some unique evolutionary innovations (i.e. horizontal tooth replacement) that allowed for a broader dietary spectrum. It was not until around the extinction of the dugongids in the western Atlantic and Caribbean region

that trichechids returned to marine ecosystems and became the most successful clade of extant herbivorous marine mammals.

However, much is still unknown regarding the morphology of these early trichechines. Future fieldwork in key localities across South America will hopefully reveal additional details of the morphology and early evolutionary history of this group.

CRediT author statement

Catalina Suarez: Conceptualization, Methodology, Investigation, Writing - Original draft preparation, Validation, Visualization. **Javier Gelfo:** Conceptualization, Methodology, Investigation, Writing - Original draft preparation. **Jorge Moreno:** Conceptualization, Methodology, Investigation, Writing - Original draft preparation. **Jorge Velez-Juarbe:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original draft preparation, Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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Appendix A. Supplementary data

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